

Variability of *Acrosterigma elongatum*, a polytypic species (Mollusca, Cardiidae)

Jacques Vidal

Laboratoire de Malacologie, Museum National d'Histoire Naturelle, 55 rue Buffon,
75005 Paris, France.

ABSTRACT

The detailed study of general features and rib structure on numerous specimens of the subfamily Trachycardiinae from the Indo-West Pacific, generally identified as *Acrosterigma elongatum*, *A. enode*, *A. serricostatum*, *A. okinawaense* and *A. wilsoni*, and comparison between them, shows that they are conspecific and belong to a polytypic species: *Acrosterigma elongatum* (Bruguière, 1789). Although there are numerous intermediate forms, six geographically distinct subspecies can be defined.

INTRODUCTION

The group in question is widely distributed in the intertropical zone of the Indo-West Pacific, and is often locally abundant. Its representatives are always readily distinguished from the other Cardiidae but they are themselves geographically variable. Many of these geographic variations are very distinct and have been considered as specifically different (as seen, for example, on plates 1- 3.). This is why several nominal species have been described in this complex: *Acrosterigma elongatum* (Bruguière, 1789), a form mainly from Philippines and Moluccas; *Acrosterigma enode* (Sowerby, 1840), a form without any tangible type specimen, interpreted very variously by subsequent authors; *Acrosterigma pulicarium* (Reeve, 1845) also lacks a type specimen and is possibly a juvenile form; *Acrosterigma serricostatum* (Melvill & Standen, 1899), a small form, probably juvenile, from Torres Strait; *Acrosterigma okinawaense* (Kuroda, 1960), a form from Japan; *Acrosterigma wilsoni* (Voskuil & Onverwagt, 1991), a distinctive form from Western Australia.

If only a small number of specimens were examined, any observer would consider these to be distinct species. However, after examination of more than 400 individuals, many of them transitional, I have concluded that they all represent a single polymorphic species: *Acrosterigma elongatum* (Bruguière, 1789).

Within this species, as shown below, four levels of variation can be observed. These are: 1)- Individual variation: The outline of the shell and rib structure can strongly vary on each individual during the growth of the shell. 2)- Collective variation: From one individual to another the above individual variation is of different intensities, both in outline and rib structure, and can be small or very marked. The combination of these variable elements leads to multiple forms in adult shells, the juvenile shells always being similar. 3)- Population variation: The above combination of characters does not occur totally at random, and it is possible to observe basic combinations, some groupings of characters, which appear more frequently. In all I have recognized six groups, each one including mainly forms close to the basic typical combination. In every area, each population is

formed mainly by individuals belonging to one dominant group, beside intermediate forms and possibly some rare other forms in other groups. 4)-Geographic variation: The dominant groups constituting the local populations vary geographically. In the Indo-Pacific, six different areas, each with distinctive shell morphology have been considered.

MATERIALS AND METHODS

The examined material comes from the collections of several Museums:

ANSP: Academy of Natural Sciences - Philadelphia.

AMS: Australian Museum - Sydney.

BM(NH): British Museum (Natural History) - London.

IRSNB: Institut Royal des Sciences Naturelles de Belgique - Brussels.

LACM: Los Angeles County Museum of Natural History - Los Angeles.

MHNG: Museum d'Histoire Naturelle de Genève - Geneva.

MNHN: Museum National d'Histoire Naturelle - Paris.

NHMV: Naturhistorisches Museum - Vienna.

NNM: Nationaal Natuurhistorisch Museum - Leiden.

USNM: United States National Museum (Smithsonian Institution) - Washington.

WAM: Western Australian Museum - Perth.

ZMA: Zoologisch Museum - Amsterdam.

More than 400 individuals were examined. Among them about 10% only are considered as juvenile (less than 7 cm in height). The origin of these specimens is from the following areas: INDIAN OCEAN: Kenya, Zanzibar, Mozambique, oriental Africa, Madagascar, Mauritius, Seychelles, Maldives, Sri Lanka, Thailand, Sumatra Indonesia, Singapore, Western Australia, Northern Territory. PACIFIC OCEAN: Japan, Philippines, Borneo, Malaysia, Moluccas Indonesia, Irian Jaya, Papua New Guinea, Caroline Islands, Marshall Islands, Wallis Islands, Tonga, Fiji, Solomon Islands, Vanuatu, New Caledonia, Queensland.

This examination includes all the type material, except for *A. okinawaense* of which, however, I was able to obtain good photographs.

Characters examined: 1)- General characters of the shell at juvenile and adult stages: general outline, symmetry or asymmetry, dimensions (H = height, L = length, W = width, always given in the same order: $H \times L \times W$), ratios between length and height (L/H), colours on the exterior and the interior. 2)- Other external features such as the structure of the the umbo, the ligament, and the pseudo-lunular area, etc. 3)- Hinge characters. 4)- Sculptural characters: a)- Rib number. b)- Structure of the ribs and interstices and nature of their ornaments. These elements are variable on a single shell according to the position of the rib on the shell and, on a given rib, according to the stage of growth, *i.e.* the position between the umbo and the ventral margin. Thus the position and ontogeny of the ornamentation must be considered. It was recorded both from the first formed part of the shell, near the umbo, and the newer part, near the shell margin. These ontogenic changes are always the same, but can have a different "gradient" according to the specimen considered, *i.e.* they can occur more rapidly or more slowly. The changes do not stop in the marginal areas at the same stage from one shell to another and consequently there are different configurations from one specimen to another.

In spite of this variability in adult specimens, the ornamentation of the the earliest stage of growth, the "juvenile stage" (corresponding to the umbonal part of the shell), is always the same and is often appreciably different from the one of the marginal part of the shell corresponding to the "adult stage". The juvenile stage is the earliest part of the post-metamorphosed shell, from the umbo, between 0.5 and 3 or 4 cm in height. In order to simplify the descriptions, the specimens with a small amount of variation in rib structure

from the juvenile stage will be called "pedomorphic", whereas those with a significant change of sculpture are called "allomorphic".

The shells are divided concentrically into four areas, each one representing about a quarter of the shell and generally having a different ornamentation. These four quarters are designated by initials: AQ = Anterior Quarter, MAQ = Medio Anterior Quarter, MPQ = Medio Posterior Quarter, PQ = Posterior Quarter. The description of ribs in the posterior quarter generally takes no account of the two or three last ribs and interstices which are often different. In addition to this, each quarter will be divided into two parts according to the stage of growth: an umbonal part representing the juvenile stage of growth, and a marginal or adult part representing the final stage of growth. The limit between these two parts is progressive and its location variable with each specimen.

SYSTEMATICS

I have subdivided the listing of denominations into synonymy *sensu stricto* and chresonymy (i.e. the subsequent usage of the synonyms) and in each of these two subdivisions I separate the correct and the incorrect usages. I have not tried to list all chresonymic references, but have restricted myself to the ones with adequate illustration, not elsewhere cited. An almost complete list of chresonyms is found in Fischer-Piette (1977).

It is not the purpose of this paper to deal with genus level problems and I provisionally adopt Wilson & Stevenson's solution, and the choice of the genus *Acrosterigma* (see 1977, pages 73-77).

Family Cardiidae Lamarck, 1809.

Subfamily Trachycardiinae Stewart, 1930.

Genus *Acrosterigma* Dall, 1900.

***Acrosterigma elongatum* (Bruguière, 1789).**

Synonyms:

Cardium elongatum Bruguière, 1789: 228.

Cardium enode Sowerby, 1840a, fig. 51; 1840b: 108.

Cardium (*Trachycardium*) *serricostatum* Melvill & Standen, 1899: 191, pl. 11, fig. 20.

Trachycardium (*Acrosterigma*) *okinawaense* Kuroda, 1960: 82.

Trachycardium wilsoni Voskuil & Onverwagt, 1991: 64, pl. 3, fig. 1.

Uncertain synonyms:

Cardium pulicarium Reeve, 1845, Sp. 102, pl. 19, fig. 102.

Cochlea nebulosa Martyn, 1786, 3, pl. 140.

Not synonyms:

Cardium magnum Linnaeus, 1758, *sensu* Clench & Smith 1944 suggested as a possible synonym by Fischer-Piette (1977).

Eleven nominal species, erroneously considered by Fischer-Piette (1977) as synonyms of *A. enode*: 1)- *Cardium arenicolum* Reeve, 1845. 2)- *Cardium gratiosum* Deshayes, 1854. 3)- *Cardium lacunosum* Reeve, 1845. 4)- *Cardium leucostomum* Born *sensu* Reeve, 1845. 5)- *Cardium maculosum* Wood, 1815. 6)- *Cardium mauritanum* Deshayes, 1854. 7)- *Cardium multistriatum* Sowerby, 1833. 8)- *Cardium nebulosum* Reeve, 1845. 9)- *Cardium*

tracendens Melvill & Standen, 1899. 10)- *Cardium tumidum* Deshayes, 1854. 11)- *Cardium unicolor* Sowerby, 1840.

Cardium flavum Linnaeus, *sensu* Fischer-Piette (1977), erroneously considered as a synonym of *Cardium serricostatum*.

Chresonymy:

Correctly attributed:

Cardium elongatum: Römer, 1869: 53, pl. 10, fig. 8 & 9.

Acrosterigma elongatum: Wilson & Stevenson, 1977: 78, pl. 5, fig. 1-4.

Trachycardium elongatum: Drivas & Jay, 1988b: 17, fig. 12.

Trachycardium elongatum: Voskuil & Onverwagt, 1991: 68, pl. 3, fig. 7-8.

Cardium enode: Römer, 1869: 59, pl. 11, fig. 9.

Vasticardium enode: Kuroda et al., 1971: 620 & 399, pl. 89, fig. 3.

Acrosterigma enode: Wilson & Stevenson, 1977: 79, pl. 5, fig. 8-9.

Trachycardium (Vasticardium) enode: Springsteen & Leobrera, 1986: 306, pl. 87, fig. 1.

Cardium (Trachycardium) serricostatum Melvill & Standen: Melvill, 1909: 75 & 133.

Vasticardium pulicarium (Reeve): Cernohorsky, 1972: 22, pl. 63, fig. 8.

Incorrectly attributed:

Trachycardium (Vasticardium) elongatum: Springsteen & Leobrera, 1986: 307, pl. 87, fig. 7 [= *Acrosterigma fidele* Vidal, 1992].

Trachycardium serricostatum: Abbott & Dance, 1982: 328 [= probably *Trachycardium luteomarginatum* Voskuil & Onverwagt, 1991: 61, pl. 2, fig. 5-6].

Trachycardium enode: Oliver, 1992: 126, pl. 23, fig 5a-b [= *T. luteomarginatum* Voskuil & Onverwagt, 1991: 61, pl. 2, fig. 5-6].

Type material

Cardium elongatum: Bruguière (1789) based his detailed description upon the specimen in Lamarck's personal collection, now stored in MHNG (Reg. No 1085/54). This shell is 95 mm high and 70 mm long (L/H= 0.74), with 39-40 ribs. According to Lamarck (1819: 9), the species "habite les mers d'Amérique?", which is certainly erroneous. Bruguière has no opinion concerning the origin of the specimen. In addition, he refers to six illustrations among which three, from Lister (1687, pl. 331, fig. 168), Chemnitz (1782, pl. 17, fig. 179) and Born (pl. 3, fig. 6-7), represent *C. magnum* Linnaeus *sensu* Clench & Smith 1944, from the American Atlantic. Among the three others, the illustration from Seba (1758, pl. 86, fig. 3) is certainly different from *C. magnum* (large size, about 40 ribs), and is probably conspecific with the shell in Geneva, and the two others (Klein, 1753: 144 and Favanne, 1784, pl. 52, fig. G) are unidentifiable. Consequently, *C. elongatum* is based upon seven syntypes belonging to at least two species. It is therefore necessary to select a lectotype. I select as lectotype of *Cardium elongatum* Bruguière, the specimen in MHNG quoted above. Its original locality is not known.

Cardium enode: Sowerby (1840b: 108) refers to only one shell figured in his Conchological Illustrations (1840a, fig. 51), stated as coming from Sri Lanka. I consider this origin as questionable, because similar forms have never been observed in the Indian Ocean (see below).

Voskuil & Onverwagt (1991: 70) assert they have discovered two syntypes of *C. enode* Sowerby from Cuming's collection in BM(NH), No 1991-044, and selected the smallest as lectotype (1991, pl. 3, fig. 9). They write "The smallest specimen, 83.5 mm high x 69 mm long x 50 mm wide, with 38 ribs, fits the type illustration and description of *Cardium enode* best". Although I have seen only photographs of these shells, I cannot agree to that for the following reasons: 1)- The selected lectotype, contrary to what they assert, does not have the dimensions of the specimen cited and figured by Sowerby. The former has the following dimensions: 83.5 x 69.0 x 50.0 mm, when the latter, as indicated by Sowerby, is 2.60 x 2.30 x 1.60 poll. [*pollex* in Latin = thumb = inch = 25.4 mm] or 66.0 x 58.4 x 40.6 mm, dimensions which correspond perfectly with Sowerby's figure, but not with any of the so-called syntypes which are too large. 2)- Not only the dimensions, but also the proportions do not fit Sowerby's indications: Sowerby's shell is less elongated ($L/H = 0.88$, versus 0.83 for the other). In addition, this shell is regularly subcircular, without any posterior truncation, when the "lectotype" is appreciably posteriorly truncated. 3)- The ornamentation is also different on both shells: on Sowerby's shell, the interstices between the ribs are extremely narrow ("*angustissimis*", as indicated), when on the "lectotype" they are somewhat wider.

Among the different subspecies of *A. elongatum* which will be described below, Sowerby's shell could belong to a group from the Pacific, when the supposed syntypes are close to the forms of the Indian Ocean.

Cardium serricostatum: Figured syntype specimen (Melvill & Standen 1899, pl. 11, fig 20) in BM(NH) (Reg. No 1899-2-23-10): one single left valve from Torres Strait, 20 mm high with 40 ribs. In my opinion it is a juvenile specimen of *A. elongatum*.

Trachycardium okinawaense: This name first appears (as *Vasticardium serricostatum okinawaense* Kuroda M.S.) in Habe (1951: 145). Kira (1955, pl.55, fig.11) figures it as *Vasticardium serricostatum* Kuroda M.S.. Kira (1959: 139) gives a description of the species, in Japanese, under the name *Vasticardium serricostatum* Melvill & Standen var., with the same illustration. Kuroda (1960: 82) describes it as a new species (in Japanese) with the name *Trachycardium (Acrosterigma) okinawaense*, and designates as type specimen the shell figured by Kira in 1955 and 1959. The shell is described in English by Kira in 1962 (page 157), still with the same figure (pl. 56, fig. 11). The dimensions of the shell given by Kira are: 59.8 x 45.0 x 42.7 ($L/H = 0.75$). The type locality is Amami Islands, without more precision. Kira's illustrated material is stored in Osaka City Museum (Natural History), not available for loan. In my opinion the figured type of *A. okinawaense* represents a small (but adult) specimen of *A. elongatum*.

Trachycardium wilsoni: The holotype of *T. wilsoni* (see Pl. 2, fig. 1a-b) is deposited in NNM in Leiden (Holland). This shell (NNM No 56583), from Broome, Western Australia, is 70.5 x 51 x 39 mm ($L/H = 0.72$), with 43-44 ribs. It is a perfect pedomorphic form of *A. elongatum*. Thirteen paratypes have been designated. Among them six from Western Australia and four from Queensland are not stored in any museum but are in private collections, and so I have been able to examine only the three deposited in museums (the following numbers are mine, in order of citation in Voskuil & Onverwagt's article): Paratype No. 4 (WAM No 732-66), from Rosemary I., Western Australia. It is 75 x 55 x 46 mm ($L/H = 0.73$), with 37-38 ribs. It is also pedomorphic and typical. Paratype No. 12 (NNM No 56584), from Fiji, is 65.0 x 47.5 x 38.1 mm ($L/H = 0.73$), with 40-40 ribs. It shows a beginning of allomorphy. Paratype No. 13 (NNM No 56585), from the Moluccas, is 79.1 x 63.1 x 38.1 ($L/H = 0.80$), with 36-37 ribs. It is a form close to Indian Ocean forms, with a slight allomorphy and a small elongation, and is rather different from the holotype. This specimen is also slightly "tuberculated" (see below).

Cardium pulicarium: The type specimen is figured by Reeve (1845, fig. 102). Apparently

it has not been traced anywhere. No locality is given. This shell could also be a juvenile specimen of *A. elongatum*.

Cochlea nebulosa: Iredale (1927: 75) took this shell, only known by the above cited figure, as type of the genus *Vasticardium*, considering it as synonym of *Cardium elongatum* Bruguière. In my opinion the drawing of Martyn is not sufficient to be sure of the real identity of the shell. In addition the rib number is 27 or 28, possible but exceptional for *A. elongatum*.

DISCUSSION

History of the interpretations of the various forms of *A. elongatum*:

As already mentioned, *Acrosterigma elongatum* is a very variable species both in its shape and in its rib structure. These two characters vary quasi-independently, leading to many different forms. In addition, juvenile specimens can look different from adult ones and can be considered as different species, as in the case of *C. serricostatum* Melvill & Standen, and probably also *C. pulicarium* Reeve.

As far as adult forms are concerned, extreme forms as mentioned above can easily be considered as specifically different:

The first error was made by Sowerby, who considered as specifically different from *C. elongatum* these almost circular forms ($L/H = 0.88$) with a different rib structure, and described a new species *Cardium enode*. However, Reeve recognized that *C. elongatum* included these "circular" forms and unusually gave two figures (1844, plate 9) for his Sp. 46 *Cardium elongatum*: figure 46 for an elongated form, and figure 47 for the circular form. Reeve wrongly attributed the name *C. enode* to a rather elongated specimen (1845, Sp. 73, fig. 73) probably because he took in consideration only one criterion to differentiate both species: the "overlapping" of the marginal serrations in the MPQ which Sowerby (1840b) also used. However this character can occur in both forms (see below).

Following Sowerby and Reeve, only rarely have two nominal species been considered, as, for example, Romer (1869) (two different species) or Hidalgo (1903) (two synonyms). The other authors generally mentioned only one of the two names (for example *C. enode* used in Japan, *C. elongatum* in the Indian Ocean, etc.) and their reasons for the choice of one name rather than the other were never specified.

Kuroda (1960) introduced a new species: *T. okinawaense*, for a form from Okinawa Is, previously identified as a subspecies of *serricostatum*, and considered it as different from those from Japan *sensu stricto* which he still identifies as *enode*. The taxon *okinawaense* is last cited by Kira (1962: 157). Habe, who had introduced it in Japan (1951: 145), does not include it in his list in 1977 (page 165). On the other hand the name *enode*, used first also in Japan by Habe in 1951, still continues to be exclusively utilized (for example: Gakken 1975: 118, Okutani *et al.*, 1989: 101). This utilization is certainly erroneous, because the Japanese specimens are among the most different forms from the one described by Sowerby as *enode* in the whole of *A. elongatum* complex.

The opinion of Fischer-Piette (1977) is not completely clear about *A. elongatum* and *enode*. It seems that he considers them as synonyms, and synonymizes them incorrectly with many other species (see above).

Wilson & Stevenson (1977) try, for the first time, to clarify the problem of *elongatum* and *enode*. They consider as *A. elongatum* the pedomorphic forms (Western Australia and Indian Ocean), and as *A. enode* the allomorphic forms (Pacific Ocean). Unfortunately they appear to ignore that Bruguière's type of *C. elongatum* is an allomorphic form corresponding to what they describe as *enode*.

In 1991, Voskuil & Onverwagt, recognizing this latter fact, attempt to solve the problem by introducing a new species (*T. wilsoni*) for the forms of Western Australia, but they retain the two additional species *T. elongatum* and *T. enode*, the latter being separated in theory with the same criteria as Sowerby (outline and "overwrapping").

Lamprell & Whitehead (1992, pl. 28-29) mention only two species in Australia: *A. wilsoni* and *A. elongatum*, but there is no mention of *A. enode*.

Finally, Oliver (1992: 126, pl. 23, fig. 5a-b) erroneously identifies as *enode* a species from the Red Sea and Indian Ocean recently identified as *T. luteomarginatum* Voskuil & Onverwagt, 1991. [= *T. marerubrum* V. & O., 1991]. This species, previously diversely interpreted, but mainly as *C. leucostoma* Born *sensu* Reeve, does not belong to the *elongatum* complex.

In the beginning of my study, when only limited material was available, I also tended to try to recognize several species in the *elongatum* complex, but my attitude changed as new material progressively filled in the gaps which might have been considered as delineating species.

DESCRIPTION

General characters:

Dimensions: *Acrosterigma elongatum* is probably the largest of all living Trachycardiinae. Dimensions of the largest specimen examined, from Port Vila, Vanuatu (BM(NH) uncatalogued): H= 139.3, L= 118, W= 89 mm. Iredale (1927: 75) based his name *Vasticardium* (synonym of *Acrosterigma*) on this character and noted a specimen 137.5 mm high from Vanikoro, here figured (pl. 3, fig. 6a-b), with 40 ribs.

Shape: Outline of the shell very variable: the young shell is not elongated, often almost circular, and equilateral. The adult shell can sometimes be roughly equilateral, ovoid or pear-shaped, rarely ellipsoidal, to even almost circular, but is more commonly inequilateral. The inequilateral shape can be due to three growth factors: (1) widening of all the posterior half or only of the MPQ, with curving of the ribs towards the posterior margin; (2) truncation of the posterior part of the shell at a variable angle with the dorso-ventral axis. When this truncation affects mainly the MPQ, the PQ looks like a wing, sometimes accentuated by the presence of a depressed radial area on the limit between the PQ and the MPQ; (3) constriction of the anterior part. The combination of both posterior and anterior straightenings can give the shell a "subrectangular" appearance, with the ribs more or less "diagonally" disposed.

The elongation of the adult shell is very variable within a population, but mainly between populations. The ratio L/H ranges from 0.70 (shell very elongated) to 0.91 (shell almost circular).

Colour: The periostracum is thin and light brown. When it is removed, the exterior of the shell is of variable colour: white, yellowish, pink, brown, with spotted or concentric darker zones. The MPQ is often darker. These colours are generally rather lusterless. The interior varies also from white to orange (mainly in the umbonal area). The margins, particularly the posterior one, are often yellow to purple.

Other external features: Umbones weakly prosogyrate; pseudo-lunular area rather narrow with thin scaled riblets near the umbos, disappearing towards the anterior margin of the shell; ligament strong and short.

Hinge characters: Hinge line moderately arched and symmetric. The juvenile shells are less arched and more symmetric. Posterior cardinal tooth (4b) in the left valve medium

sized (length about half of the width of the hinge), rather high and bulky. The foundation of the anterior lateral teeth is very weakly curved, (not "hooked").

Sculptural characters:

a)- Rib number: The general mean number is 37 (range 32-44). This mean number varies according to areas and populations. For example in New Caledonia it is about 36 (range 32-39), whereas in Western Australia it is about 40 (range 35-44).

b)- Structure of the ribs and interstices and nature of their ornaments:

i)- Juvenile stage of growth: PQ: 5 to 8 ribs, high, round-topped and square-sided, bearing, on their posterior half, regularly set and slightly curved scales (distance about 1 to 2 mm between each scale), making a 45° angle with the axis of the rib. The anterior edge is strongly serrated by thinner scales, the first ribs of the zone being also finely serrated on their posterior edge, between the main scales. The scales and the border serrations project over the interstices which are deep and almost as wide as the ribs. Other parts of the shell: With the exception of a very small umbonal area, the medial and anterior parts of the shell are ornamented with very high ribs, with parallel "vertical" flanks, both with their upper edges crenulated with relatively sturdy regularly set rugae. These rugae join more or less across the top of the ribs, from one side to the other, forming transverse folds more or less depressed in the axis of the ribs. On the borders of the ribs, these structures overhang the flanks and the interstices, which are slightly narrower than the ribs. The "vertical" lower part of the flanks and the "horizontal" bottom of the interstices are generally smooth and never noticeably notched nor striated. The above features of the juvenile part are constant and common to all the shells, until the shell reaches several cm in height. Then the features change, and this evolution can be small or large leading to very different structures, according to several processes :

ii)- Adult stage of growth with small evolution from the juvenile stage: PEDOMORPHIC forms: (see pl. 1, fig. 2). PQ: The ribs and the interstices remain approximately the same, and keep the main scales on their posterior half. These scales remain up to the ventral margin, becoming more and more parallel to the ribs, and more and more located on the posterior border of the ribs. The serrations of the anterior edge of the ribs disappear progressively. Other parts of the shell: The evolution from the older stage is less important: the ribs remain high and square-sided, regularly transversally ridged on the top, with serrated upper edges. Then the top of the ribs becomes flat and smooth, except on the AQ, where the transverse ridges still remain with an imbricated structure. The interstices are still large. The last ribs of the MPQ often become asymmetric, bending forward, with their posterior flank wider and exceptionally somewhat striated.

iii)- Adult stage of growth with important evolution from the juvenile stage: ALLOMORPHIC forms: (see pl. 1, fig. 3 and 4). PQ: A significant evolution leads to the progressive modification of the ribs. This modification always starts with the disappearance of the border scales and serrations; after that the ribs lose their sharp edges and their relief is reduced. The ribs then become flatly rounded and even entirely rounded, all the zone becoming practically smooth or even with the previous interstices retaining in relief. Three sorts of development can occur: 1. The posterior main scales of the ribs disappear. After that, the posterior "vertical" flank of the ribs is progressively reduced, disappears and is replaced by a scar line. Finally, the anterior flank of the ribs disappears also and the ribs become flatly rounded or even entirely rounded, sometimes depressed in their axis and often almost indistinct. 2. When the anterior flank of the ribs has been reduced, the anterior part of the flattened ribs subsides progressively along a longitudinal, more or less distinct

gash, and gets down to the level of the remaining interstices. The consequence is that the interstitial zones widen out at the expense of the ribs. These latter zones are often of a different colour (white, pink, purple etc.) from the colour of the residues of the ribs (darker, brown etc.). This "bicolouring" is, I think, very species-specific. The "pseudo-interstitial" zone often remains depressed and flat (flat-bicolouring, see pl. 1, fig 3). 3. In that case, the interstices become decidedly lighter in colour, but do not widen. Their bottom cambers, forming like a riblet between the residual main ribs. Sometimes too, the residual main ribs still lower and practically disappear, the above "riblets" then becoming the only prominent zones and so forming "new ribs" instead of the previous interstices (ribbed-bicolouring, see pl. 1, fig. 4). Other parts of the shell : In the anterior half of the shell, the ribs tend to be flatter, wider and the interstices narrower. In the MPQ the ribs become lower and tend to lose their sharp edges and marginal serrations. Their profile is extremely variable: flatly rounded, triangular, entirely rounded, entirely flat and even depressed, with an onward slope or not, etc. The interstices vary also strongly from largely open to reduced to "deep narrow cuts" (Reeve 1844: Sp 46).

Summarized comparison between pedomorphic and allomorphic structures:

	Pedomorphic	Allomorphic
PQ-	1- Ribs high, square-sided. 2- Large scales on posterior half of top of ribs. 3- Interstices deep, large.	1- Ribs low and flatly rounded, even with no relief. 2- No scales, ribs smooth. 3- Interstices shallow or even prominent, widening or not, often lighter coloured (bicolouring).
MPQ-	1- Ribs high, flat-topped, square-sided. 2- Edges of top of ribs sharp, finely crenulated. 3- Interstices deep and large (1/2 of ribs width).	1- Ribs low, flatly-rounded or flat, rounded or triangular. 2- Edges of top of ribs rounded and smooth (no crenulations). 3- Interstices shallow and generally narrow.

Overlapping of the interstices in the MPQ margin:

Generally, in the different species belonging to the genus *Acrosterigma*, when the shell is closed, the extremities of the interstices on the ventral margin are on a level with the extremities of the ribs, or even are placed a little below. This is not the case in many specimens of *A. elongatum*, where the bottoms of the interstices, in the MPQ margin, are much longer than the ribs and overlap above the ribs extremities. Sowerby, who describes this phenomenon for the first time (1840b: 108: "ribs terminating in very strong overlapping teeth"), considers it as a main characteristic of a new species, *Cardium enode*, different from *C. elongatum*. This opinion was adopted by some authors, in particular by Wilson & Stevenson (1977: 80).

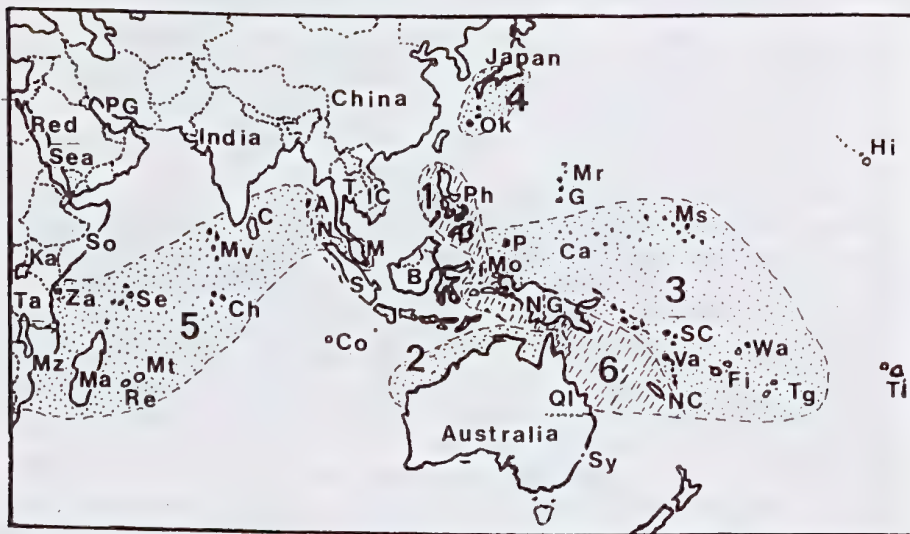
The observations I have made do not allow me to follow such opinions. On the contrary I observed that: a)- The phenomenon is not constant: in a same population it is variable from one specimen to another and can be absent. b)- I have observed it, more or less abundantly, in all groups of *A. elongatum* (which will be described below), including the typical forms of Western Australia, except the Japanese forms.

Tuberculated forms of *Acrosterigma elongatum*:

In certain populations, among normal specimens with the ribs of the MPQ smooth on the top, some specimens may occur with tubercles on the top of the ribs of this quarter. These tubercles, more or less conical and regularly set, are homologous to the main scales of the adjacent PQ. They are generally visible to the naked eye. The scales of the PQ, situated on the posterior part of the ribs, progressively migrate to the central part and become tubercles in the anterior part of the the PQ and in the MPQ. This phenomenon extends on the last ribs of the MPQ, or on the whole quarter (*i.e.* 6-7 ribs of the MPQ involved), and possibly on several ribs of the anterior part of the PQ where the tubercles replace the scales. It is very variable in extension but always limited to intermediate growth stages (end of juvenile and more or less part of adult). These very characteristic tuberculated specimens are rare. As a coincidence, the lectotype of *C. elongatum* Bruguière is one of them. In addition, I was able to observe only a few specimens in nine populations from Zanzibar (see pl. 1, fig.7), Madagascar, Timor Sea, Japan (see pl. 2, fig. 5a-b), Philippines, Moluccas, Papua New Guinea, Vanuatu (see pl. 1, fig. 8), and New Caledonia.

Distinction between *A. elongatum* and the other species of the genus *Acrosterigma*:

All forms of *A. elongatum* are easily distinguishable from other species of this genus and misidentifications have been rare. *A. elongatum* principally differs from the congeneric species by the combination of the following characters: 1)- In the earliest formed part of the shell, the ribs are always high, square-sided and strongly ornamented. 2)- The tops of the ribs of the MPQ and posterior part of the MAQ in the adult forms are always smooth (except in the "tuberculated" forms). 3)- Interstices and flanks of the ribs are never appreciably striated or notched. 4)- The mean rib number is about 37. 5)- The basement of the anterior lateral teeth is very slightly curved, never "hooked". 6)- The interstices and ribs of the PQ can have different colour patterns ("bicolouring" phenomena). 7)- The overwrapping of the MPQ margin is rare in the other species.



Map 1: Distribution of *Acrosterigma elongatum* and its six subspecies: 1. Subspecies *elongatum*. 2. Subspecies *wilsoni*. 3. Subspecies *enode*. 4. Subspecies *cipangense*. 5. Subspecies *indioceanum*. 6. Subspecies *coralense*.

Subspecies of *Acrosterigma elongatum*:

As stated above, the different forms of *A. elongatum* in the adult shells are the result of different combinations of two varying groups of characteristics: shape and rib structure. From one given combination to another, the shell can look very different. All the theoretically possible combinations are not realized and all the existing forms are not present everywhere. In each region one can observe a single predominant type of combination, co-occurring with other types and intermediates. These predominant types of combinations can be arranged in six main groups which correspond to six geographic regions. In each of these regions the shells, in general, have certain common characters of shape and rib structure, criteria which have been utilized to separate the 6 different groups. In addition the shells can have some other common characters like colour and number of ribs.

I refer now to Mayr *et al.*, (1953): "Species that consist of two or more subspecies are called polytypic species" (p. 26). "Subspecies are geographically defined aggregates of local populations which differ taxonomically from other such subdivision of a species" (p.30). "What is taxonomically different can be determined only by agreement among taxonomists. The difference must be sufficiently great so that it is possible to identify the great majority of specimens without knowledge of their provenience. For this purpose many taxonomists adhere to the 75 per cent rule" (p.31). According to these definitions, it seems to me that the above six regions correspond with six subspecies. The rare specimens of these groups which are found in non-corresponding regions and some uncommon specimens which do not fit any of the six groups, are considered as "individual variants". These proposed subspecies are defined as follows (see Map 1):

Acrosterigma elongatum elongatum (Bruguère, 1789).

Pl. 1, fig. 1a-b, fig. 3 and fig. 7.

Taxonomic characters: Elongated to moderately elongated (L/H range 0.74-0.81), slightly truncated or not, elliptic or more or less pear-shaped (expansion of the MPQ with curvature of the ribs backwards). Appreciably allomorphic in the MPQ with lowering of the ribs, rounding of their sides and reduction of the interstices, and with a significant "flat-bicolouring" in the PQ.

Other characters: Mean number of ribs 38.8 (range 36-42). External colours generally rather darker than in the adjacent regions: yellow, brown, reddish. The MPQ is generally darker still. Internal colours white or pale yellow with almost always purple coloured margins, mainly the posterior side.

Range: Philippines and Moluccas.

Acrosterigma elongatum wilsoni (V. & O., 1991)

Pl. 2, fig. 1a-b and fig. 2.

Taxonomic characters: Very elongated (L/H range 0.72-0.74), strongly truncated posteriorly and slightly crushed anteriorly ("subrectangular"). Limit between the PQ and the MPQ more or less depressed and the PQ somewhat "winged". This depression corresponds with an important ridge inside the shell. Rib structure pedomorphic.

Other characters: Mean number of ribs 39.6 (range 35-44). External colour relatively darker than in the west Indian Ocean province, internal colour comparable.

Typical specimens in collections: a)- A specimen from Western Australia 68.5 x 49.0 x 37.5 (L/H= 0.72), orange yellow and pink, with strong "overlapping" in the MPQ margin (Vidal coll., MNHN). b)- A "record" specimen from Exmouth Bay, Western Australia: 108.4 x 79.0 x 60.8 (L/H= 0.73), (NNM).



Plate 1. Fig. 1a-b. Lectotype here selected of *Cardium elongatum* Bruguière, right valve, Bruguière's specimen from unknown locality, L = 70.0 mm (Lamarck coll., MHNG 1085-54). Fig. 2. A specimen intermediate between subsp. *wilsoni* and *indioceanum*, right valve, from Cape York, Australia, L = 59.0 mm (WAM 4774-68). Fig. 3. A specimen of subsp. *elongatum*, left valve, from unknown locality, (Jousseau Coll., MNHN). Fig. 4. A right valve of subspecies *enode* from Port-Vila, Vanuatu, L = 107.3 mm (Vidal coll., MNHN). Fig. 5. A left valve of subsp. *coralense*, with only 25 ribs, from Noumea, New Caledonia, L = 41.1 mm (Vidal coll., MNHN). Fig. 6. A left valve of subsp. *coralense*, with only 29 ribs, from Noumea, New Caledonia, L = 47.0 mm (Vidal coll., MNHN). Fig. 7. An individual variant close to subsp. *elongatum*, tuberculated form, right valve, from Zanzibar, L = 72.4 mm (Rousseau coll., MNHN). Fig. 8. A specimen of subsp. *enode*, tuberculated form, right valve, from Port Vila, Vanuatu, L = 60.0 mm (Vidal coll., MNHN).

Range: North West Cape, Western Australia, Gulf of Carpentaria to Torres Strait, North Queensland.

***Acrosterigma elongatum enode* (Sowerby, 1840).**

Pl. 1, fig. 4 and fig. 8; pl. 3, fig. 6a-b, and fig. 7a-b.

Taxonomic characters: Moderately elongated to almost circular (L/H range 0.79-0.91); rarely posteriorly truncated; the MPQ often more or less inflated. Strongly allomorphic with significant "ribbed bicolouring" in the PQ; in the MPQ ribs flat, with rounded top edges, almost touching (very narrow interstices).

Other characters: Mean rib number 37.5 (range 35-40). No special colour characters. The forms of this group are generally large (the largest of all the subspecies), heavy and with a wide hinge zone and large teeth.

Type: As there is no type of the species, I select as neotype of *C. enode*, a specimen from Port-Vila (Vanuatu), deposited in the MNHN (Pl. 3, fig. 7a-b): L/H = 0.88, 38 ribs.

Typical specimens in collections: a)- As *T. elongatum* a "record" specimen 139.3 mm high, from Port-Vila (Vanuatu), (BM(NH)). b)- From Wallis Is a specimen 129 mm high (Hombron & Jacquinot coll. 1841, MNHN).

Range: Caroline, Marshall, Wallis, Tonga, Fiji, Vanuatu, Santa-Cruz, Solomon and East coast of New Guinea. No records of the species from Mariana nor from Eastern central Pacific: Hawaii, Polynesia.

***Acrosterigma elongatum cipangense* subsp. nov.**

Pl. 2, fig. 5a-b.

Taxonomic characters: Moderately to not elongated (L/H range 0.77-0.85), not or slightly posteriorly truncated. Quasi-perfectly pedomorphic. Ribs very high and interstices wide (sometimes as wide as ribs or more).

Other characters: Mean number of ribs 39.0 (range 37-41). External colour generally uniform and light, beige to pale yellow. Internal colour white.

Types: Holotype: Pl. 2, fig. 5a-b, a specimen from Tosa, Japan (Hirase coll., USNM 346125). Paratype No 1: a specimen from Tosa, Japan, deposited in the MNHN (Staadt collection, 1969), H = 90.0, L = 71.7, W = 60.5, (L/H = 0.80) with 38-39 ribs.

Remark: *A. okinawaense*, because its rib structure, looks different from this subspecies.

Typical specimen in collections: a)- A specimen from Japan labelled as *T. enode* (Huffman coll., LACM No 13491).

Range: Japan, Northern limit: Boso Peninsula, near Tokyo.

***Acrosterigma elongatum indioceanum* subsp. nov.**

Pl. 2, fig. 3a-b; pl. 3, fig. 1 and fig. 2a-b.

Taxonomic characters: Moderately elongated (L/H range 0.78-0.83); elliptical and equilateral to rather inequilateral with dilatation of the posterior half; not or more or less posteriorly truncated. Pedomorphic to slightly allomorphic in the PQ (often a slight "bicolouring" develops in the anterior part of the ribs, since the posterior part keeps the pedomorphic scales); in the MPQ the height of the ribs is reduced but they generally keep their sharp and finely crenulated top-edges, mainly on the posterior side; the interstices remain relatively wide.

Other characters: Mean number of ribs 36.6 (range 32-42). External colours light: white, beige, yellow, pink, rarely orange, sometimes with more coloured splashes purple or brown. Internal colour often entirely white, with sometimes umbonal cavity yellow, and rarely a coloured posterior margin.

Type: Holotype: a specimen from Mombassa, Kenya, deposited in the MNHN (Pl. 2, fig. 3a-b): $H = 73.1$, $L = 57.4$, $L/H = 0.79$, with 35 ribs.

Range: Indian Ocean: East coast of Africa from Mozambique to Kenya and Zanzibar, Islands of the Indian Ocean (Madagascar, Réunion and Mauritius, Seychelles, Chagos, Maldives, and according to Tidaker *et al.* (1986: 176) Andaman and Nicobar), Sri Lanka, north-east Sumatra and one sample from the east coast of Malaysia. Not recorded in the Northern Bay of Bengal, in Somalia, Gulf of Aden, Red Sea and Persian Gulf. The absence of records in these tropical waters may seem strange. Nevertheless, the excellent figures 8 and 9, pl. 13, of Savigny, 1812, of a shell from the Egyptian Red Sea, looks very much like a form of this subspecies.

***Acrosterigma elongatum coralense* subsp. nov.**

Pl. 1, fig. 5 and 6; pl. 3, fig. 3.

Taxonomic characters: Rather elongated (L/H range 0.77-0.81), well allomorphic in the MPQ, but the allomorphism remains at first stage in the PQ (rib structure change but no "bicolouring"); the result is that the PQ and the MPQ have a similar rib structure.

Other characters: Mean number of ribs 36.0 (range 32-39, with two exceptions of 25 and 29). External colour rather uniform and light, generally pink, sometimes yellow or white.

Type: Holotype: a left valve from Noumea, New Caledonia, deposited in the MNHN (Pl. 3, fig. 3): $H = 75.0$, $L = 57.7$, $L/H = 0.77$, with 35 ribs.

Typical specimen in collections: A specimen from Queensland (WAM 160-88).

Range: New Caledonia and North Eastern Australia from North Queensland to Keppel Bay (Queensland).

Individual variants:

They are isolated specimens which do not belong to the subspecies of the area where they are. They can be classified into three categories:

1)- Specimens belonging to another known subspecies. Example (1): A specimen of the subsp. *elongatum* found in Zanzibar (pl. 1, fig. 7). Example (2): A specimen of the subsp. *wilsoni* found in New Caledonia, $81.8 \times 62.2 \times 48.0$, (Hargraves Coll., AMS C.47774).

2)- Specimens with intermediate characters between two known subspecies. Example (1): A specimen intermediate between *wilsoni* and *indioceanum* found in Cape York, Queensland (pl. 1, fig. 2 and pl. 2, fig. 4). Example (2): A specimen with general feature of *wilsoni* and sculpture of *coralense*, Smith Point, N. T., Australia, (AMS C.101959).

3)- Specimens with unusual characters or unusual combination of characters. Example (1): Specimens very elongated, strongly "subrectangular", with a mean allomorphism in the posterior half (no bicolouring). Several isolated specimens found in the *coralense* area: (1a): A specimen from New Caledonia (pl. 2, fig. 6a-b). (1b)- A specimen from Whitsunday Passage, Queensland (Jackson coll., AMS C.84353). Example (2): A specimen with all the ribs of the posterior half entirely rounded, with semi-circular profile, and "open" V-shaped interstices (a very unusual rib structure for this species), from Noumea, New Caledonia (pl. 3, fig. 4). Examples (3): Some specimens, elongated, slightly subrectangular, allomorphic with bicolouring in the PQ, but still pedomorphic in the MPQ. In the whole shell the interstices are wide and of a decidedly lighter colour than the ribs. (3a): A specimen from Santa Rosa, Cebu Is, Philippines (pl. 3, fig. 5a-b). (3b): Two specimens from Siasi Reefs, Sulu Sea, Philippines, forming probably a local mini-population (Vidal coll., MNHN). (3c)- The specimen from Ticao, Philippines, figured by Sowerby as *C. elongatum* (1840a, fig. 49), not traced, could belong to these forms. Example (4)- Considered as individual

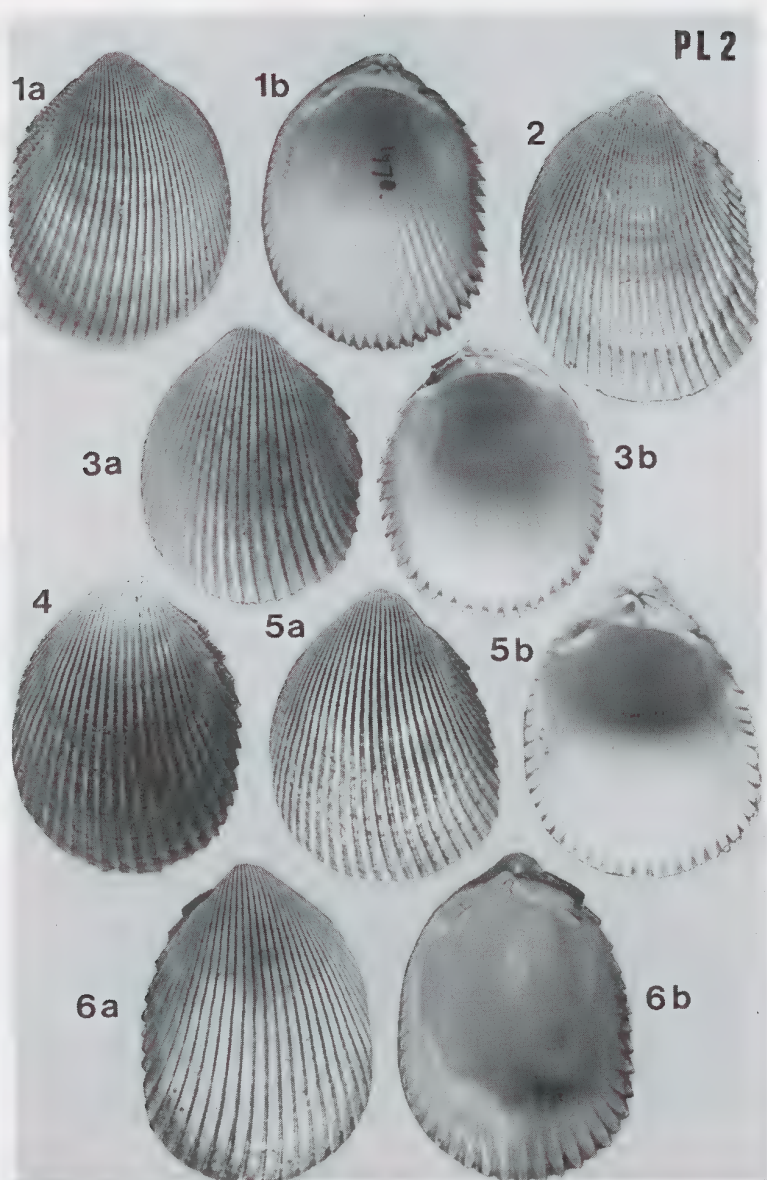


Plate 2. Fig 1a-b. A specimen of subsp. *wilsoni* from Broome, Western Australia, holotype of *Trachycardium wilsoni* Voskuil & Onvervagt, L = 51.0 mm (NNM 56583). Fig. 2. A left valve of subsp. *elongatum* with a beginning of allomorphy, from Karratha, Western Australia, L = 56.1 mm (Vidal coll., MNHN). Fig. 3a-b: Selected holotype of the subspecies *indioceanum*, a specimen from Mombassa, Kenya, L = 57.4 mm (Poppe coll., MNHN). Fig. 4. A specimen intermediate between subsp. *wilsoni* and *indioceanum*, left valve, from Cape York, Australia, L = 59.0 mm (WAM 4774-68). Fig. 5a-b. Selected holotype of subsp. *cipangense*, from Tosa, Japan, L = 81.5 mm (USNM 346125). Fig. 6a-b. An individual variant, right valve, from New Caledonia, L = 66.0 mm (Staatd coll. 1969, MNHN).

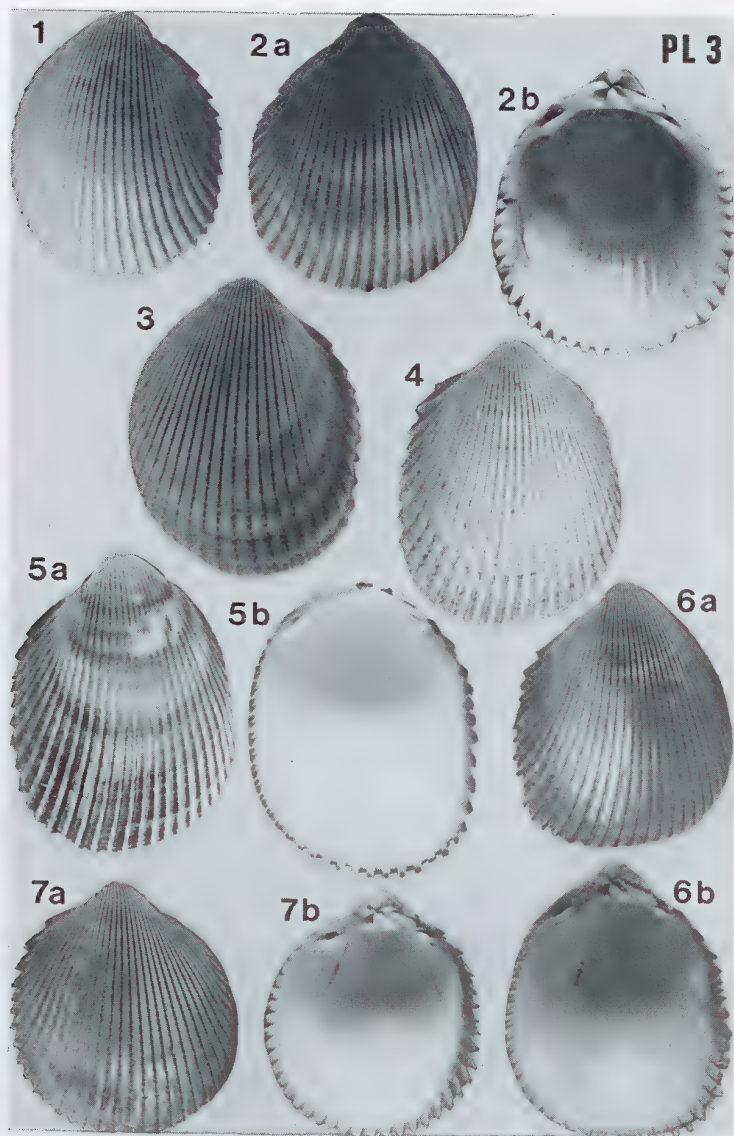


Plate 3. Fig. 1. A specimen of subsp. *indioceanum*, left valve, from unknown locality, L = 56.4 mm (Soc. d'Océanogr. coll., MNHN). Fig. 2a-b. A right valve of subsp. *indioceanum* from Singapore, L = 70.0 mm (Stadt coll. 1969, MNHN). Fig. 3. Selected holotype of the subspecies *coralense*, a left valve from Noumea, New Caledonia, L = 57.7 mm (Vidal coll., MNHN). Fig. 4. An individual variant, left valve, from Noumea, New Caledonia, L = 59.4 mm (Vidal coll., MNHN). Fig. 5a-b. An individual variant, right valve, from Cebu I., Philippines, L = 69.5 mm (Vidal coll., MNHN). Fig. 6a-b. A specimen of subsp. *enode*, right valve, from Vanikoro, Santa Cruz Is. (AMS C.52173), cited by Iredale (1927: 75), L = 110.4 mm. Fig. 7a-b. A specimen of subsp. *enode*, selected neotype of *C. enode*, right valve, from Port-Vila, Vanuatu, L = 92.6 mm (Vidal coll., MNHN).

variants as far as rib number is concerned, two specimens of the subspecies *coralense*, from Noumea area, New Caledonia (pl. 1, fig. 5-6), with respectively 25 and 29 ribs.

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